



## Male hyraxes increase countersinging as strangers become ‘nasty neighbours’



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Many territorial animals interact less aggressively with neighbours than with strangers, a phenomenon known as the ‘dear enemy’ effect, although some species show the opposite behaviour. Rock hyraxes, *Procavia capensis*, are social mammals that communicate via a rich acoustic repertoire. Male hyraxes produce elaborate advertisement calls (i.e. songs) both spontaneously and in response to occasional attention-grabbing events (e.g. pup screams, agonistic interaction), as well as to conspecific male songs. When replying to conspecific songs, male hyraxes tend to respond more to familiar males than to strangers, reflecting the ‘nasty neighbour’ effect. Our study relates to the general question of why some species respond aggressively towards neighbours, while others are more aggressive towards strangers. We hypothesized that male hyraxes eventually familiarize themselves with a stranger, subsequently perceiving its intentions as highly threatening and deserving of a vocal response. To simulate the presence of a stranger in the area we exposed wild hyrax groups to playbacks of natural songs of unfamiliar hyraxes. Male rock hyraxes became more likely to reply to a stranger’s song over time, but this was independent of the number of times they heard the song. This suggests that either (1) the threat presented by a stranger increases when it is no longer perceived as transient or (2) because listeners do not physically encounter the stranger, they perceive replying aggressively as a low-risk response. Our work implies that species may demonstrate a range of condition-dependent behaviours instead of a dichotomy between the ‘nasty neighbour’ and ‘dear enemy’ strategies.

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Territorial animals generally respond less aggressively to neighbours than to strangers, a phenomenon termed the ‘dear enemy’ effect (Getty, 1987). In accordance with this effect, selection favours a set of one or several strategies that fit game theory (e.g. limited war strategy; Smith & Price, 1973), wherein a territory owner can learn to recognize and respect the territory of others (Parker, 1974). Gains and losses from interactions may predict the intensity of a territory owner’s responses to neighbours and strangers. Territorial competitors’ interactions are commonly explained by two hypotheses: (1) the familiarity hypothesis and (2) the threat level hypothesis. The familiarity hypothesis argues that familiar neighbours reduce aggression towards each other to enable better management of time and energy, and thus decrease the risk of injury (Catchpole & Slater, 2008). According to the ‘asymmetric law of attrition’ model, as the opponents come to

know one another better, errors in identity and purpose become less likely, and the intensity of aggression decreases (Ydenberg, Giraldeau, & Falls, 1988). Alternatively, the ‘fighting to learn’ model asserts that animals engage in fighting to learn about their opponents and therefore familiar neighbours fight very little because they have little to learn about each other (Getty, 1989).

In accordance with the threat level hypothesis, the relative threat presented by neighbours and strangers influences the intensity of a territory owner’s aggressive response (Temeles, 1994). Thus, a consideration of the relative threats presented by neighbours versus strangers may explain why, in some species, territory owners may increase aggression towards familiar neighbours (Müller & Manser, 2007; Temeles, 1990). This ‘nasty neighbour’ effect has been demonstrated when neighbours compete intensely and residents outnumber strangers. For example, banded mongooses, *Mungos mungo* (Müller & Manser, 2007) and song sparrows, *Melospiza melodia* (Moser-Purdy, MacDougall-Shackleton, & Mennill, 2017) respond more strongly to neighbouring groups than to strangers, as neighbours threaten the

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owner's territory, compete for mates and participate in lethal fights. A tit-for-tat conditional strategy may also lead to increased aggression towards neighbours. For example, male red-winged blackbirds, *Agelaius phoeniceus* (Olendorf, Getty, Scribner, & Robinson, 2004) and hooded warblers, *Wilsonia citrina* (Godard, 1993) tend to increase aggression towards familiar individuals that intrude upon their territories.

The rock hyrax, *Procavia capensis*, is a social mammal that lives in mixed-sex groups. In our study area (Ein Gedi, Israel) a hyrax group comprises several males (one mature immigrant resident and several young, local late dispersers) and 3–20 females with their pups (1–3 pups/female; Bar Ziv, et al., 2016). Males reach puberty at the age of 17–24 months, and, soon after, voluntarily and gradually leave their birthplace, or occasionally are forced to disperse by the resident male (Hoeck, 1989; Koren, 2000). Breeding is seasonal and synchronized (Mendelssohn, 1965), and females mate with multiple males, possibly to mask paternity (Bar Ziv, et al., 2016; Koren & Geffen, 2009). Bachelors live mostly solitarily on the periphery of colonies and in rare cases may congregate into bachelor groups (Koren, Mokady, & Geffen, 2006). Bachelors interact with the mixed-sex groups mainly for mating and during feeding (Koren, Mokady, & Geffen, 2008).

Hyrax males are typically not territorial and do not monopolize food resources (Bar Ziv, et al., 2016). However, when resident males reside with a group of females they display aggressive behaviour and dominate bachelors that approach the group females (which can also occur outside of the breeding season; Koren et al., 2008). Moreover, during the mating season only the resident males are observed mate guarding the older and experienced females, and displaying aggression towards any bachelor males that attempt to court and mate with those females that were mothers in previous years (Bar Ziv, et al., 2016). Accordingly, emphasizing the defence of females as a resource (i.e. rather than defending space), a territory may be defined as 'floating' or 'moving': a spatiotemporal area that a group occupies and that remains centred on the group as it moves (Kaufmann, 1983). Thus, we view the hyrax social group as a moving area that is kept free of bachelor males by the resident's aggressiveness towards them.

Rock hyraxes employ a rich vocal repertoire as an important means of information transfer (Fourie, 1977). Adult males communicate using long-distance vocalization signals that we term 'songs' (Koren & Geffen, 2009): these are variable, complex signals that express individuality and are likely to make the caller familiar to the listeners (defined as song by Spector, 1994). Song conveys information communicated via acoustic characteristics through parallel pathways: body size, weight, condition, social status, identity and hormonal profile of the singer are encoded in the song (Koren & Geffen, 2009, 2011). Male hyraxes perform complex songs throughout most of the year and singing gradually increases during March–April (with an average number  $\pm$ SD of  $3.815 \pm 2.76$  singing events per day), peaks in July ( $7.9 \pm 7.45$ ) and decreases in frequency shortly after. Both resident and bachelor males sing when they are spatially separated and have no physical contact with other males (Koren et al., 2008). In our study area, individual males sing naturally every day and male-to-male countersinging comprises about 25% of overall songs performed (Demartsev, Ilany, et al., 2016; Ilany, Barocas, Koren, Kam, & Geffen, 2011). During countersinging, songs are more elaborate than songs that males perform spontaneously or without any observable external trigger (Demartsev et al., 2014). Resident males tend to reply at a high rate to bachelors whereas bachelors reply at a low rate to residents, while other factors such as body weight and tenure on site have no effect on listeners' reply rate (Demartsev, Ilany, et al., 2016). In many species, singers may countersing with conspecifics to signal aggression (Hyman, 2003), suggesting that hyrax countersinging

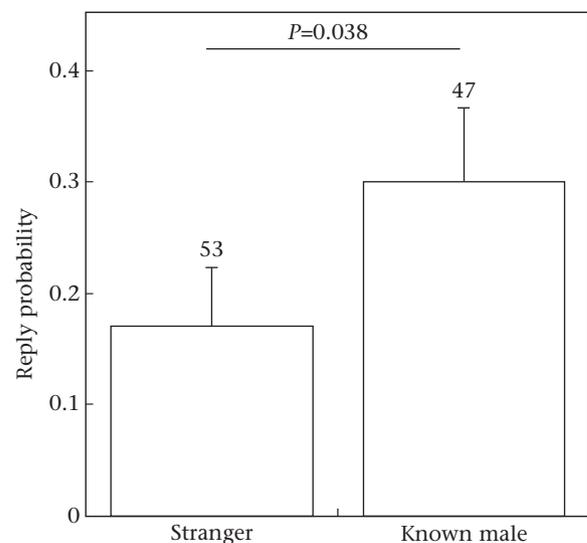
probably constitutes an escalated mutual signalling between males, enabling them to advertise their relative social and physical traits without the need for actual fighting (Demartsev, Ilany, et al., 2016; Koren & Geffen, 2009).

Recently, Demartsev, Ilany, et al. (2016) demonstrated that male hyraxes reply more readily to familiar males than to strangers (Wald  $\chi^2_1 = 4.3$ ,  $P = 0.038$ ; Fig. 1), contrary to the 'dear enemy' effect. Here we investigated the 'nasty neighbour' effect further by conducting playback experiments simulating the arrival of a stranger into the area. The stranger hyrax's songs were played for several consecutive days/weeks, and the rate of response by local male hyraxes was recorded. Following the observations of Demartsev, Ilany, et al. (2016) and the 'nasty neighbour' hypothesis, we posited that once the local males had become familiar with the signal (i.e. song) of a stranger, they would reply to it, probably because they perceived the stranger either as a new threat with the intention of settling in the area or as a potential audience. We expected that a greater number of playbacks would facilitate the extraction of information and make the stranger more familiar to the listeners (the familiarization hypothesis). However, because playbacks over a longer time are indicative of settling in the area, this could therefore also be interpreted as a high threat (the threat level hypothesis). Thus, we predicted that the reply levels of individual local male hyraxes would rise both over time and with frequency of playback, and would be higher in response to a song of a stranger that had been a resident (i.e. residing with a group of females) before.

## METHODS

### Ethical Note

This study was conducted under a permit from the Israeli Nature and Parks Authority. The annual permit numbers are 2011/38061, 2012/38400, 2013/38803, 2014/40185, 2015/40768, and 2016/41174. Throughout the 18-year field study, no long-term stress or interference effects were detected in individual animals or in the overall population. Both population numbers and the integrity of the specific social groups in the research area remained stable.



**Figure 1.** The probability ( $\pm$  SE) of replying to a playback of a local male (i.e. known individual) or a stranger. Values above bars denote number of playbacks. Data taken from Demartsev, Ilany, et al. (2016).

## Field Protocol

The study was conducted at the Ein Gedi Nature Reserve in Israel (31°28'N, 35°24'E) as part of a long-term project that began in 1999. The data for the current study were collected between 2011 and 2016. During each field season (April–August), hyraxes were observed for 4–5 days per week. Field procedures followed previously published protocols (Demartsev et al., 2014; Demartsev, Bar Ziv, Shani, Goll, Koren, & Geffen, 2016; Demartsev, Ilany, et al., 2016). In the present study, hyraxes were observed during their morning and afternoon activity hours (morning activity starts at dawn and continues until early noon and afternoon activity begins once their living area becomes shaded and continues until dusk). We used social groups that had been studied for several years. We defined resident males as those that were observed in a stable association with a group of females, sharing sleeping dens and feeding sites; and bachelor males as those that showed no stable association with other individuals and were observed only in brief interactions with females during the mating season (Barocas, Ilany, Koren, Kam, & Geffen, 2011).

## Vocalization Recording and Playback Experiments

Male song is composed of bouts that contain three consistently repeated syllables: wail, chuck and snort (Koren & Geffen, 2009). Average song duration is about 1.5–2 min and on average a song contained  $29.7 \pm 18.7$  ( $\pm$ SD) bouts and  $169.3 \pm 100.5$  ( $\pm$ SD) syllables. Previously recorded songs were played via a FoxPro Scorpion X1B speaker using a TX200 remote control (FOXPRO Inc., Lewis-town, PA, U.S.A.). To eliminate the possibility of a male hearing a playback of an acquaintance, only playbacks of hyraxes (individually recognized and behaviourally observed) that had died several years before and could not have been encountered, or playbacks recorded at a distant research site (minimal distance between sites is 3 km) were played. Since 1999 only two cases of hyraxes moving between the two sites have been recorded. Accordingly, strangers were never present at the site where their playbacks were used for our trials. All songs used in our playbacks were performed by adult males (Appendix Table A1) and recorded in our research area. The criteria of recording quality and song duration were used to determine the songs used for the playback experiments, with an average song duration of 1.5–2 min (Demartsev et al., 2014). The playback sound pressure level (SPL) was calibrated in several preliminary trials to match the level of natural hyrax singing, which has previously been identified as approximately 80 dB at the source (Ilany, Barocas, Kam, Ilany, & Geffen, 2013; Ilany, Barocas, Koren, Kam, & Geffen, 2013).

Playback experiments were performed following our previously published protocol (Demartsev et al., 2014; Demartsev, Bar Ziv, et al., 2016; Demartsev, Ilany, et al., 2016). For each social group, the position of the speaker was randomly varied among several different locations. The playback was initiated after an identified male hyrax or a group of at least four hyraxes were observed within a 20–30 m radius of the speaker. Sixteen different songs performed by 16 different male hyraxes (i.e. strangers) were used. We played a song of the same stranger to the same group on several occasions over an average period of  $19 \pm 10$  days. A total of 79 playbacks (16 series of three to seven sequential playbacks) were played to nine different groups over no more than 36 days, at an average interval of  $5 \pm 4$  ( $\pm$ SD) days. In each trial series, we played a single song from a different stranger to each social group. The speaker was activated only if no natural hyrax vocalization had been heard for at least 5 min, to ensure that the focal individual was responding only to the playback stimulus. To avoid desensitization, no more than two playbacks were performed per group per day. We define

countersinging as a singing response that occurred if at least one male started countersinging within 2.5 min of the playback (Demartsev et al., 2014). We combined our data with previously published data by Demartsev, Ilany, et al. (2016), whose experiments had been conducted in an identical manner.

## Statistical Analysis

We examined three relevant independent variables as effects on the reply rate (i.e. the dependent variable) in our experiments: number of days from the first playback (i.e. cumulative time from first play), number of days from the last playback, and the number of playbacks played. To determine whether the physical and/or social characteristics of the stranger also affect the reply rate over time, we evaluated the effect of male residency status (i.e. resident or bachelor) and age of the strangers we used for the playbacks.

We used a logistic regression within the framework of the generalized estimating equations (GEE). GEE is an extension of generalized linear models (GLM) for correlated data (i.e. mixed model), and is specifically designed for repeated measures within the same subjects (Overall and Tonidandel, 2004). We set individual/group and playback identities as random effects in all GEE analyses. The Wald  $\chi^2$  was used for testing the significance of each effect. Multiple comparisons were conducted using the sequential Bonferroni correction. GEE model fitting was done in SPSS (version 22, SPSS Inc., IBM, Armonk, NY, U.S.A.).

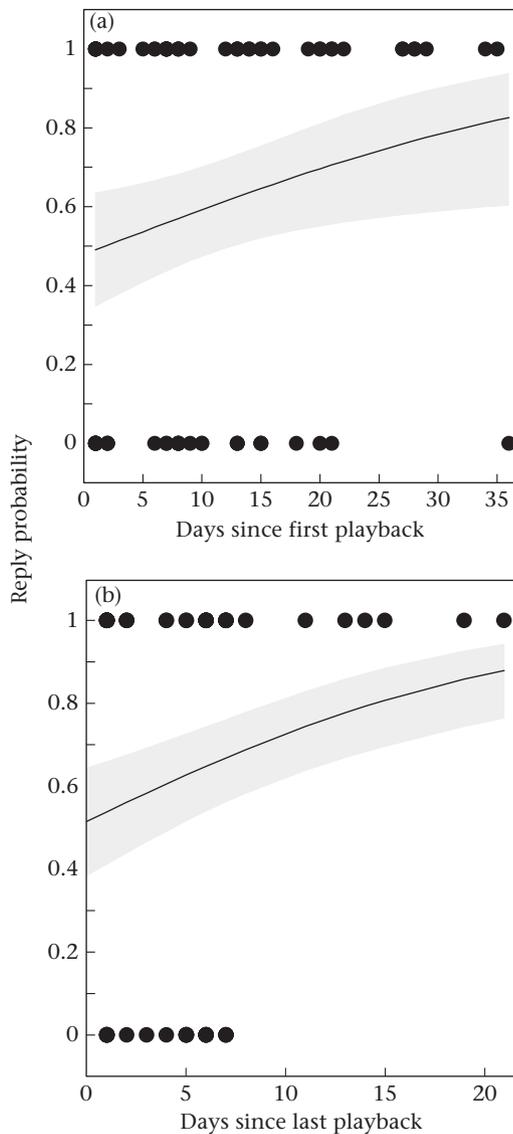
## RESULTS

The reply rate to stranger song increased significantly both with time (cumulative time from first playback: Wald  $\chi^2_1 = 5.4$ ,  $P = 0.020$ ; Fig. 2a) and with the number of days that had passed since the latest playback (Wald  $\chi^2_1 = 6.4$ ,  $P = 0.011$ ; Fig. 2b). However, the number of times a song was played did not affect the reply rate (Wald  $\chi^2_1 = 0.6$ ,  $P = 0.416$ ).

We also evaluated the effect of the stranger's residency status and age on the reply rate (Table 1). Our extended models showed that reply rate increased significantly with time (i.e. estimate > 0), but again the number of playbacks was not a good predictor for the reply rate (Table 1). The age of the stranger had no effect on reply rate in any of the models we examined. The reply rate to a stranger that had been a resident before (estimated marginal mean of reply rate in all models was  $0.74 \pm 0.02$  ( $\pm$ SD)) tended to be higher than to a novel bachelor ( $0.58 \pm 0.02$ ), but the differences were not significant (Table 1). The interactions between stranger residency status and the various effects associated with time were nonsignificant in all three models (Wald  $\chi^2_1 = 3.1$ ,  $P = 0.080$ ; Wald  $\chi^2_1 = 1.3$ ,  $P = 0.249$ ; Wald  $\chi^2_1 = 1.1$ ,  $P = 0.293$  for models 1, 2 and 3, respectively). The lack of interaction in all models suggests that the reply rate of males increased with time towards strangers that had been residents in a different location or several years before and towards bachelor strangers.

## DISCUSSION

Supporting our initial prediction, we found that the probability of replying to a stranger (i.e. to a novel song) increased over time, regardless of the former stranger's residency status, but did not increase with the number of playbacks performed. Moreover, listeners' reply rates tended to be higher to the song of a novel hyrax that was a resident before than to that of a novel bachelor. In accordance with the 'nasty neighbour' effect, aggressive response to a neighbour has been previously explained by the threat level hypothesis (Brunton, Evans, Cope, & Ji, 2008; Müller & Manser, 2007; Schradin, Schneider, & Lindholm, 2010; Temeles, 1990,



**Figure 2.** The probability of replying to a stranger hyrax natural song as a function of the number of days passed (black line) since (a) the first and (b) the last playback. Each dot represents the outcome of a single playback. Shaded areas represent 95% confidence intervals for the trend. Parameters were estimated using GEE.

**Table 1**  
The effect of number of days from the first playback, number of days from the last playback, the number of playbacks played, stranger residency status and stranger age on the reply rate to playbacks

Model	Estimate	Wald $\chi^2_1$	P
<b>Model 1</b>			
Number of days from the first playback	0.049	3.9	0.048
Stranger residency status	-0.688	3.3	0.068
Stranger age	-0.178	0.6	0.427
<b>Model 2</b>			
Number of days from the last playback	0.116	13.7	<0.0001
Stranger residency status	-0.557	1.9	0.087
Stranger age	-0.152	0.4	0.370
<b>Model 3</b>			
Number of playbacks played	0.176	1.8	0.184
Stranger residency status	-0.940	3.5	0.061
Stranger age	-0.230	0.8	0.363

N = 66 in all models.

1994). We offer three possible explanations for the local male hyraxes' tendency to reply to an established stranger (defined as an adult male that had arrived and settled in the area). First, listeners need time to familiarize themselves with a stranger's signal before responding (familiarization hypothesis). Second, a stranger presents only a potential threat to the local males. However, when a local male no longer perceives a stranger as transient, or views it as a novel audience, the level of threat rises and the local male responds (threat level hypothesis). Third, listeners that do not physically encounter the stranger eventually become accustomed to his signal, and may seize the opportunity to signal aggression with minimal risk (acclimation hypothesis).

#### The Familiarization Hypothesis

Individual recognition requires familiarization with a signal (Tibbetts & Dale, 2007). In rock hyraxes, the acoustic features and temporal data of a song can individually identify males (Koren & Geffen, 2011), and males discriminate between stranger and neighbour song (Demartsev, Ilany, et al., 2016). While information about differences in fighting ability can be gained in a physical encounter (Enquist & Leimar, 1983), aggressive signalling transfers information about the signaller's willingness to escalate the interaction and its fighting ability (Zahavi, 1977), and can be as effective as a physical attack in intimidating opponents and winning contested resources (Van Staaden, Searcy, & Hanlon, 2011). In male rock hyraxes, songs indicate the singers' social rank (Koren & Geffen, 2009), a measure correlated with the potential outcome of physical clashes with other males (Gammell, de Vries, Jennings, Carlin & Hayden, 2003). Furthermore, male hyraxes can obtain information about their opponents' traits from other males' songs (Demartsev, Bar Ziv, et al., 2016). Therefore, we hypothesized that it may take listeners time to learn a new opponent's characteristics (such as weight, age, social rank and residency status), and the more often the local male is exposed to a stranger's song, the more information he might be able to extract from it. However, the number of times that the stranger's song was played did not have a significant effect on reply rate, so it is unlikely that males became more likely to respond to strangers' songs because of familiarization.

#### The Threat Level Hypothesis

Another explanation for the delayed response to a stranger can be derived from the threat level hypothesis. Accordingly, the greater intensity of a response may be related to differences in the threat posed in terms of fighting ability and potential losses from encountering an intruder (Temeles, 1990). Mature dominant male hyraxes produce a harsh sound in their song, associated with aggression and dominance (Koren & Geffen, 2009), thus communicating a higher threat level (Zahavi, 1979). Male hyraxes can be aggressive towards each other, and close encounters between males may result in chases or fights that can lead to injury and death (Barocas et al., 2011). Consequently, local males may initially not reply to a stranger's calls because an error in the evaluation of an opponent could result in a serious fight and injury.

It has been shown that where fighting is costly, contestants tend to assess the value of the resource and the resource-holding power of their opponent, and withdraw without escalation if they are unlikely to win. For example, female lions, *Panthera leo*, carefully adjust their behaviour according to the number of individuals in their group versus those in the opposition (McComb, Packer, & Pusey, 1994). Similarly, low levels of aggression observed within coalitions of male lions, which may suffer high costs in direct competition for oestrous females, have been interpreted within a

game theory framework rather than that of kin selection (Packer & Pusey, 1982). In our system, a strange male in the area might have been perceived as having been established for longer when more time had passed between two consecutive playbacks. Consequently, over the long term, local males could have stopped relating to a stranger as transient, and perceived it as an established competitor for both mating and residency (Bar Ziv et al., 2016; Koren & Geffen, 2011; Koren et al., 2008). We predicted that the longer the stranger remained in the area, the greater threat he would represent as a competitor to the local males. Our finding that the rate of reply tended to be higher to an established stranger thus offers support for the threat level hypothesis.

#### *The Acclimatization Hypothesis*

Because the male hyraxes we studied had never physically encountered or seen the stranger in our playback trials, we suggest an alternative, but not necessarily mutually exclusive, explanation that the local males did not initially respond to the stranger because they sought first to gather more information. Such information can be acquired during social interactions at shared feeding sites, in bachelor groups, or around the groups' moving areas, although not observing the stranger in social interaction may also be informative. Singing can be heard from across a great distance (e.g. up to 500 m; Koren et al., 2008), and male hyraxes can sing from discrete locations, without being seen. Additional information can be acquired either through personal encounters, or by monitoring the outcome of others' interactions with the stranger (i.e. eavesdropping; McGregor, 1993; Naguib & Todt, 1997; Oliveira, McGregor, & Latruffe, 1998; McGregor & Peake, 2000), which can have far-reaching effects, such as altering reproductive decisions (Mennill, Ratcliffe, & Boag, 2002; Otter et al., 1999) or assessing predation risks, for example (Danchin, Giraldeau, Valone, & Wagner, 2004). Nevertheless, in our case, the males never encountered the stranger in social situations and were therefore unable to accumulate additional information to that available from the song. Given that there was no visual signal supporting the vocal one, listeners may have become accustomed to the signalling male song and regarded the threat of a fight to be minimal because the signaller (i.e. stranger) was never in their proximity. Consequently, the local males may have seized the opportunity to transmit an aggressive signal with little to no risk involved, as singing has very low energetic cost (Ilany, Barocas, Kam, et al., 2013), but may have fitness consequences. Accordingly, the acclimatization hypothesis may also explain the males' tendency to reply more to familiar strangers over time. Further work is required to determine whether hyraxes increase their response as the stranger becomes a competitor, or because the risk of physical retaliation decreases as time passes without a physical encounter.

This work continues our long-term research on communication strategies and dynamics of hyrax male–male countersinging behaviour (Demartsev et al., 2014; Demartsev, Bar Ziv, et al. 2016; Demartsev, Ilany, et al. 2016). We have shown that over time males change their response tactics to the signals of unfamiliar males. This change is possibly dictated by the differing levels of perceived threat and/or by the need to acquire additional information regarding the opponent. The data presented here indicate that the classical dichotomy between the 'nasty neighbour' and 'dear enemy' strategies can potentially represent two extreme ends of a graded scale, as species may not exhibit one absolute tactic but instead demonstrate a range of condition-dependent behaviours. As shown in European rabbits, *Oryctolagus cuniculus*, the 'dear enemy' behaviour is weakened by simulating repeated territorial intrusions by neighbours (Monclús, Saavedra, & de Miguel, 2014), a result that resembles the pattern observed in our rock hyraxes, in

which the countersinging behaviour towards a stranger increased over time. Further study of competition tactics in other species could be important in elucidating the role of conditional effects (e.g. time, location, resource availability) on the relationships between competitors.

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#### **Supplementary material**

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2017.10.002>.

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## Appendix

**Table A1**

Group ID, number of playback sets, the number of playbacks played using each set and the characteristics (i.e. age and residency status) of the strangers used for the playback

Group ID	Series ID	No. of playbacks	Stranger age	Stranger status
A15	S1	7	6	Bachelor
A15	S2	5	5	Resident
A11	S5	3	Not known	Not known
A11	S6	3	4	Bachelor
A11	S7	3	4	Bachelor
A11	S8	4	Not known	Not known
D11	S15	7	4	Bachelor
D11	S19	6	Not known	Not known
D13	S11	3	5	Bachelor
D15	S9	4	6	Resident
HC15	S21	3	5	Bachelor
K15	S22	7	4	Bachelor
S15	S24	7	7	Resident
S15	S25	4	2	Bachelor
T15	S26	6	4	Bachelor
T15	S27	7	4	Bachelor